A Review of Host Specificity in *Tanaorhamphus longirostris* (Acanthocephala: Neoechinorhynchidae)[1]

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ABSTRACT. Of 13 species of fish recorded as hosts for the acanthocephalan, *Tanaorhamphus longirostris* (Van Cleave 1913), only two regularly contain mature worms. These are the gizzard shad (*Dorosoma cepedianum* (Lesueur)) and the threadfin shad (*D. petenense* (Günther)). To date, only one species of intermediate host, the calanoid copepod, *Diaptomus pallidus* Herrick, has been reported. In Caesar Creek Lake, Ohio, where the parasite is known to exist, of 15 species of planktonic crustaceans examined, only *D. pallidus* contained the cystacanth of *T. longirostris*. Comparison of geographic distributions and ecological and behavioral factors suggests that this association (i.e. worm, shad, copepod) represents a relatively new or developing relationship that may not yet fit closely the classical requirements for strict host specificity. Feeding behavior and host gut morphology may be the combination of factors that provides for reproductive success of *T. longirostris* in shad.

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INTRODUCTION

The acanthocephalan *Tanaorhamphus longirostris* was first described by Van Cleave (1913) as a parasite of the gizzard shad (*Dorosoma cepedianum* (Lesueur)). Van Cleave (1931) lists the following synonymies: *Neorhynchus longirostris* (Van Cleave) 1913, *Eorhynchus longirostris* (Van Cleave) 1914, and *Neoechinorhynchus longirostris* (Van Cleave) 1916. For the next 70 years, although sporadically reported from fishes, intermediate hosts for this form were unknown. Hubschman (1983) reported that the calanoid copepod, *Diaptomus pallidus* Herrick, served as an intermediate host in Caesar Creek Lake, Ohio.

Analysis of host records for *T. longirostris* suggests that this worm does not parasitize a wide range of fish species. Usually the data also disclose both low prevalence and low intensity of infection. In addition, a common feature of such records is the absence of mature worms in many of the fish species examined. There is, however, an apparent high degree of specificity in the relationship between *T. longirostris* and shad of the genus *Dorosoma* (Van Cleave 1916; Jilek 1978). Likewise, although there remains much to be learned about the life cycle, to date only *D. pallidus* is known to harbor the cystacanths. There may be specificity in this relationship as well.

Shulman (1954) reviewed specificity among fish parasites. He proposed five factors that were favorable for the development of host-specificity: 1) close contact of parasite with host (he refers to the duration of contact during the life cycle); 2) degree of morphological and physiological adaptation to host (the greater the adaptation, the stronger the specificity); 3) the presence in the host of some morphological, ecological, or physiological peculiarities; 4) time (he refers to the length of association in evolutionary time); and 5) stability of the environment and constancy of food supply (in this he refers to tissue sites within the host and limits the concept to *sexually* mature parasites).

This paper will examine some of the factors and conditions that may bear on the apparent host-specificity of *T. longirostris*. In turn, these will be discussed in light of the categories proposed by Shulman.

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HOST RECORDS

A list of fish species reported to contain *Tanaorhamphus longirostris* is given in Table 1. A new host record added at this time is the fathead minnow (*Pimephales promelas*) which was collected from Caesar Creek Lake, Ohio on 1 July 1981.

The case for specificity in fish is not readily apparent from a simple list of host species. Collection records disclose, however, that two species have been regularly reported to harbor mature specimens of *T. longirostris*. These are the gizzard shad (*Dorosoma cepedianum*) and the threadfin shad (*D. petenense*). Most authors comment that the reverse is usually true. That is, fish species other than these two shad species contain worms that are usually dead or immature.

There are two exceptions to this observation. First is a paper by Van Cleave (1931) where he reports examining a collection given to him by Dr. P. H. Simer. He comments that *T. longirostris* in *D. cepedianum* "represents one of the most striking examples of host specificity that has been discovered among acanthocephalans in fishes." He also reported that the Simer collection had only two specimens of *T. longirostris*. One was from the type host, *D. cepedianum*, and the other from an unspecified buffalo fish (*Ictiobus* sp.). He did not comment on the condition or maturity of the worm.

Another report of host species for *T. longirostris* other than shad is provided by Bangham and Venard (1942) for fishes in Reelfoot Lake, Tennessee. In that paper, they recorded two specimens of *T. longirostris* obtained (one each) from a channel catfish (*Ictalurus punctatus*) and the fulton catfish (*I. anquilla*). Since *I. anquilla* is now considered to be the same as *I. punctatus* (Scott and Crossman 1973), this represents one additional host species for the worm.

Tanaorhamphus longirostris is known to be established in Caesar Creek Lake, Ohio (Hubschman 1983, 1985, Wilson and Hubschman 1985). A list of crustacean zooplankton species examined from that lake in 1981, 1982, and 1983 is given in Table 2. Only the calanoid copepod, *Diaptomus pallidus*, has thus far been found to serve as an intermediate host for *T. longirostris*. Although the list provides only negative information, it does suggest a basis for suspecting intermediate host specificity. In addition, the list is important because it was compiled during a 3-year study (unpublished) of that zooplankton community and was not simply a result of casual sampling. If or when additional intermediate hosts are discovered, contrasts or comparisons may be drawn between the plankton community in Caesar Creek Lake during 1981–1983 and the newly reported system.

HOST RANGES

Tanaorhamphus longirostris is an intestinal parasite peculiar to North American fishes (Van Cleave 1931). The combined distribution records for the worm, the copepod intermediate host, and the gizzard shad, the type definitive host, are shown in Figure 1. The parasite records

TABLE 1

Fish reported to contain Tanaorhamphus longirostris.

Common Name	Scientific Name	References
Bluegill sunfish	*Lepomis macrochirus*	Hubschman 1983, Jilek 1978.
Bluntnose minnow	*Pimephales notatus*	Hubschman 1983.
Buffalo	*Ictiobus* sp.	Van Cleave 1931.
Channel catfish	*Ictalurus punctatus*	Bangham & Venard 1942, Jilek 1978, Samuel et al. 1976.
Fathead minnow	*Pimephales promelas*	New record
Fulton cat	*Ictalurus anquilla*	Bangham & Venard 1942.
Gizzard shad	*Dorosoma cepedianum*	All authors listed.
Largemouth bass	*Micropterus salmoides*	Jilek 1978.
River Carpsucker	*Carpiodes carpio*	Samuel et al. 1976.
Spotfin shiner	*Notropis spilopterus*	Hubschman 1983.
Threadfin shad	*Dorosoma petenense*	Arnold et al. 1968, Hopkins 1966.
White bass	*Morone chrysops*	Samuel et al. 1976.
White crappie	*Pomoxis annularis*	Hubschman 1983, Jilek 1978.

Table 2

Limnetic Zooplankton Examined from Caesar Creek Lake, Ohio, 1981–1983.

Cladocera	Copepoda
Bosmina longirostris (O. F. M.)	Calanoida
Ceriodaphnia quadrangula (O. F. M.)	*Diaptomus pallidus* Herrick
Chydorus sphaericus (O. F. M.)	Cyclopoida
Daphnia ambigua Scourfield	*Cyclops vernalis* Fischer
Daphnia retrocurva Forbes	*Cyclops bicuspidatus thomasi* (Forbes)
Daphnia parvula Fordyce	*Euclycops agilis* (Koch)
Diaphanosoma birgei Korniek	*Mesocyclops edax* (Forbes)
Leptodora kindtii (Focke)	*Orthocyclops modestus* (Herrick)
	Tropocyclops prasinus mexicanus Kiefer

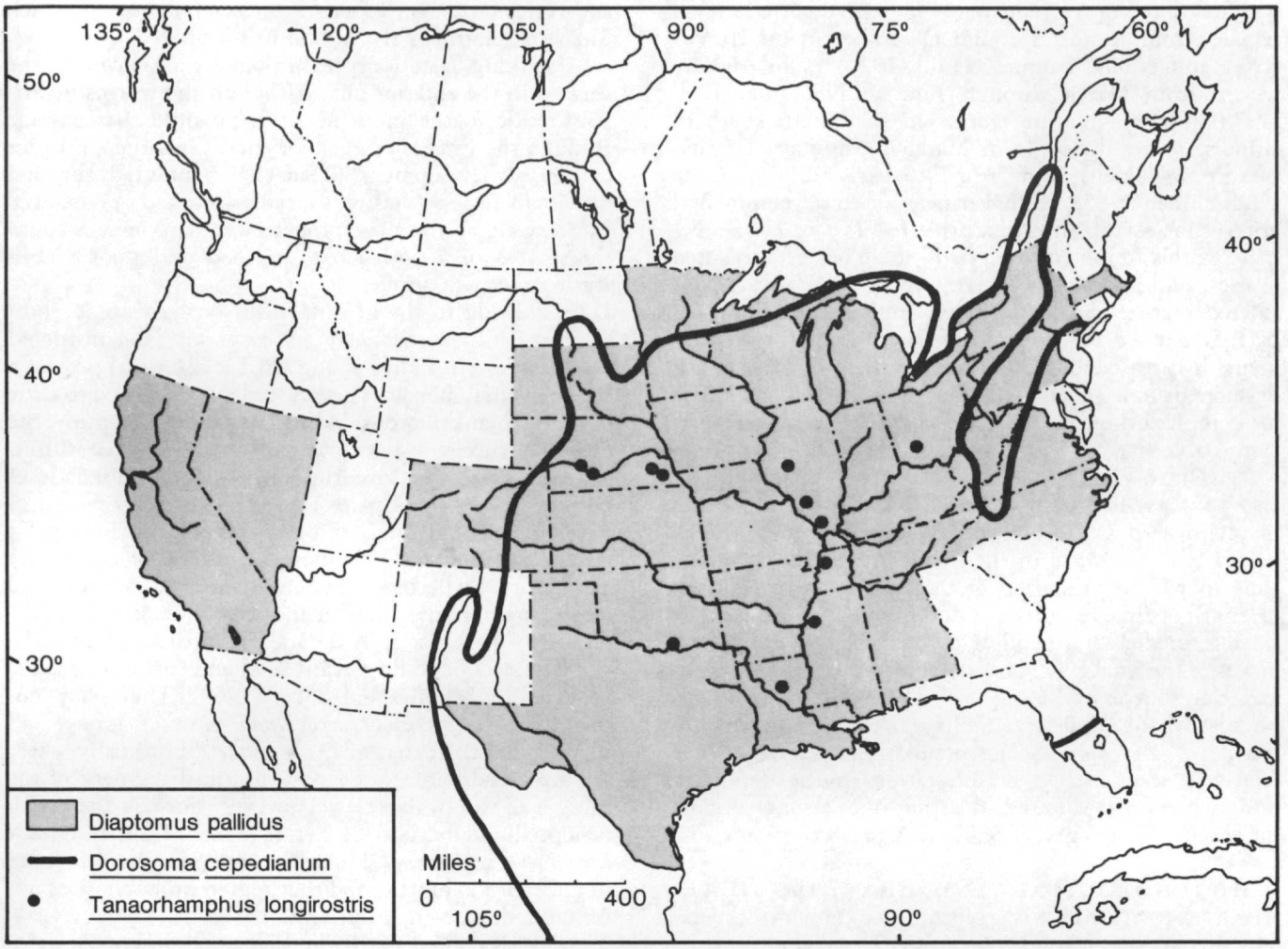

FIGURE 1. Native distribution of *Dorosoma cepedianum* (solid line), states in the U.S. recorded for *Diaptomus pallidus* (shaded area), and collection sites for *Tanaorhamphus longirostris* (closed circles).

were plotted from the reports listed in Table 1. The range of the gizzard shad is intended to show the native distribution provided by Lee et al. (1980). Although minor range extensions have been reported, this map is sufficient to show that the reported distribution of the parasite does not exceed that of the shad. The range of the calanoid copepod, *Diaptomus pallidus*, reflects a list of state records provided to me by Dr. A. Robertson (personal communication).

SPECIFICITY OF SHAD

At this point, it is important to review the evidence for host specificity of *Tanaorhamphus longirostris* since it was first suggested by Van Cleave (1931). An example of this specificity was provided by Arnold et al. (1968) for the parasites of fishes of Louisiana. Of the 52 fish species examined, *T. longirostris* occurred only in the gizzard shad and the threadfin shad. Bangham and Venard (1942) examined 43 fish species from Reelfoot Lake, Tennessee. They found *T. longirostris* in only one species of fish other than the gizzard shad. This was the channel catfish (*Ictalurus punctatus*) of which they examined 44 individuals, finding one worm in each of two fish. Van Cleave (1931) also reported one specimen of *T. longirostris* from an unidentified species of buffalo (*Ictiobus* sp.). Since that time, other authors have reported finding *T. longirostris* in species of fish other than *D. cepedianum* and *D. petenense* (Table 1). In each case, however, live or sexually mature specimens were found only in the shad. In no case was *T. longirostris* found in another fish species, where infected shad were not also members of the same community. Likewise, I have found no record of *T. longirostris* outside of the known geographic distribution of either shad or the host copepod.

The occasional presence of *T. longirostris* in fish species other than shad may be a result of ingestion of infected shad by the other host. However, among the gizzard shad that I examined from Caesar Creek Lake, no fish less than 13.5 cm total length (TL) contained worms (Hubschman 1985).

FACTORS FAVORABLE FOR THE DEVELOPMENT OF HOST SPECIFICITY

Shulman (1954) identified five factors that favor the development of host specificity. Each of these is discussed below with reference to the published data on *T. longirostris* and its known hosts.

DURATION OF CONTACT. A review of the literature disclosed that *T. longirostris* may be found in gizzard shad in any month of the year. However, within a given population, there appears to be a seasonal cycle in which mature worms occur for a relatively short period. This

was first noted by Van Cleave (1916) who reported gravid females from August through December in his Illinois River collections. Samuel et al. (1976) found mature worms from March through June in Nebraska. Jilek (1978) reported mature worms in shad from southern Illinois in the period from March to August. I found mature specimens from April to early July in Ohio (Hubschman 1985). In that paper, I used developmental criteria for establishing maturity for *T. longirostris*. Female worms in the "ovarian ball" stage with fragmented ovaries, and males with active cement glands were considered mature. Since the physiological condition of a parasite may be difficult to confirm from mounted specimens, it is reasonable to assume that reproducing worms developed under conditions that were at least adequate for completion of the life cycle and were therefore host-compatible.

Van Cleave (1916) concluded: "The demonstrable presence of a seasonal cycle in the life history of a parasite involving two or more hosts is dependent upon a) longevity of the parasite in the final host: b) extent of the time in which infestation of the final host may occur; c) length of time required for development of the larva in the intermediate host; and d) seasonal changes in the food habits of the final host, or active migration of the host to and from sources of infestation." Therefore, it should not be disturbing that seasonality in occurrence of *T. longirostris* may vary among populations. However, the relatively short period of infestation in the definitive host, wherever it is found, does not offer strong support for specificity in light of Shulman's first criterion.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATION TO HOST. Nothing is known of the extent of physiological adaptation by *T. longirostris* to its shad hosts; hence, this facet of adaptation cannot be evaluated here. We can speculate that physiological adaptation to the intermediate host may be more demanding. The shelled acanthor must emerge successfully from the egg capsule and immediately adjust to the gut environment of the copepod. It must then burrow through the gut wall and successfully adjust to the conditions of the hemocoel in which significant development takes place. Thus, greater specificity may occur in the copepod than in the shad.

Shulman (1954) pointed out that among parasites of the digestive tract, specificity is usually more weakly developed than in sexually mature parasites of other organs. In terms of morphological adaptation, aside from being relatively small, *T. longirostris* does not exhibit striking or peculiar specialization.

HOST PECULIARITIES. The ability to speculate on differences among calanoids is limited because, to date, only *Diaptomus pallidus* has been demonstrated to host the worm. In the Caesar Creek Lake collections *D. pallidus* was the only calanoid copepod (Table 2). A stronger hypothesis could be established if other calanoid copepods were present. Lake Erie provides an interesting situation since shad and several species of calanoid copepods occur there (Watson 1976). *Tanaorhamphus longirostris* has not been reported from Lake Erie (Bangham 1972, Dechtiar 1972). On the other hand, this may reflect the fact that *D. pallidus* is rarely found in Lake Erie (Smith and Fernando 1978, Robertson and Gannon 1981) which further strengthens the notion of specificity.

A striking peculiarity exhibited by *Dorosoma* is the gizzard in the anterior gut. Although the worms invariably reside in the intestine, it is possible that passage through the gizzard triggers or conditions the worm for continued development. Read (1972) pointed out that development of a parasite is usually initiated or enhanced by some signal from the proper host. This may account for success of *T. longirostris* in shad and poor viability in other fish species.

In addition to the gizzard, shad do have some noteworthy features that may or may not be considered peculiarities. Initially, young shad ($\leq$26 mm) possess a supraterminal mouth. This presumably is related to their obligate planktivorous habit. At about 26 mm, the mouth assumes a terminal position. Shad $\geq$30 mm possess a distinctly subterminal mouth characteristic of bottom feeders (Heinrichs 1982). During this period of development and later, the gut increases in length. It begins as a comparatively short gut typical of a carnivore and eventually becomes the long, complex, twisted, and looped organ of the adult. The latter condition is characteristic of herbivores. A detailed comparison of the digestive tracts of adult gizzard shad and threadfin shad is provided by Schmitz and Baker (1969). They point out that the intestine of *D. cepedianum* is much longer and more coiled than that of *D. petenense*. Specifically, there are marked differences beyond the third segment of the midgut of the two species. However, since *T. longirostris* is normally found in the anterior region of the midgut at least in *D. cepedianum* (Hubschman 1985), the difference in gut morphology beyond that region probably does not influence host compatibility.

Adult shad are not strict herbivores, however. Descriptions of food habits of gizzard shad confirm that adult shad are often omnivorous (Bodola 1966, Drenner et al. 1982, Jester and Jensen 1972, King et al. 1977, Pierce and Wissing 1981). Indeed, examination of the gut contents of shad from the same population will disclose dramatic shifts from zooplankton and organic detritus to sand, algae, or insect exuviae. It may be just that combination of a behavioral trait and a morphological feature that provides the "peculiar" condition required to satisfy Shulman's third factor. In this case, feeding on zooplankton (and therefore the intermediate host) is linked to the digestive processes associated with a gut which is characteristic of herbivores.

The feeding behavior of shad may be a feature that, while enhancing the possibility for success of the worm once ingested, discourages initial capture of the intermediate host. If this is the case, it would account for the usual low intensity and prevalence of *T. longirostris* in shad. Planktivorous fishes are usually considered to be size-selective when grazing on zooplankton. This notion has usually been assumed in studies of the impact of fish on zooplankton community structure following the Brooks and Dodson (1965) model. However, negative selection of *Diaptomus* by plankton-feeding young walleyes (*Stizostedion vitreum vitreum*) was proposed by Houde (1967). Later, Cramer and Marzolf (1970) confirmed negative selection of *D. pallidus* by gizzard shad. The studies of Drenner et al. (1982) demonstrated that under experimental conditions, gizzard shad in fact enhanced

the populations of *Diaptomus pallidus*. This apparently resulted from the avoidance behavior of the copepod rather than the expected size-selection by the predator. Since it seems that gizzard shad are poor sight feeders as adults, these two factors in combination may result in a low proportion of *Diaptomus* among the food species ingested. On the other hand, planktivorous bluegill sunfish (*Lepomis macrochirus*) depend heavily upon sight feeding (Hairston et al. 1982). Among sight feeders, the probability of ingesting an infected copepod may be enhanced by altered behavior of the crustacean itself. While there is no direct evidence available to support this in *Diaptomus*, both color change and altered behavior have been reported for isopods (Muzzall and Rabalais 1975, Seidenberg 1973). I suspect that both appearance and behavior are altered in *Diaptomus* infected with cystacanths. On several occasions, I examined small white crappies (*Pomoxis annularis*) that contained a disproportionate number of infected copepods among undigested gut contents.

LENGTH OF ASSOCIATION. From the records to date, and the distribution pattern of the hosts, it seems probable that the relationship between *T. longirostris* and its fish hosts is new and developing and therefore of short duration on an evolutionary time scale. Shulman (1954) noted that host specificity is commonly weakly developed in the early stages of a parasite. This may be especially true for the larval or infective stages, but may also apply to immature forms of the sexual stage. If the latter is the case, it may explain why *T. longirostris* occurs as an immature form in several species of fish and is found only as a sexually mature form in shad. Van Cleave (1931) cautioned that the frequency (or in this case infrequency) of occurrence of *T. longirostris* cannot be taken to signify that it is or is not common to a region. In any case, the distribution of reported worm collections does not exceed the known range of either the shad or the copepod host (Fig. 1). *Tanaorhamphus longirostris* is not only limited to North America, but is apparently confined to the Mississippi drainage.

The ancestral stock for this worm may have lived in brackish water. It could have been brought from the brackish water environment by shad that dispersed up the Mississippi River Valley. Two observations support the possibility that the locus of origin for *T. longirostris* may be the Gulf of Mexico. First, according to Amin (1985), a close relative of *Tanaorhamphus* is the genus *Atactorhynchus*. The type species, *A. verecundus*, was described from sheephead minnows (*Cyprinodon variegatus*) taken from the upper reaches of Galveston Bay, Texas (Chandler 1935). *Tanaorhamphus longirostris*, the only species in the genus, shares many morphological similarities with *A. verecundus*. Although the intermediate host for the latter is apparently unknown, the fish host, *C. variegatus*, is a coastal species occupying shallow, brackish-to-freshwater habitats, and is reported to tolerate extreme changes in temperature and salinity (Lee et al. 1980). Since *D. cepedianum* and *D. petenense* are known to enter brackish environments, either or both may have brought the worm to lakes and streams of the interior of the United States.

STABILITY OF TISSUE SITE WITHIN THE HOST. The fifth factor relates to the stability of the parasite's environment and constancy of food supply. This condition clearly varies by degree for different tissue sites. The stability of environment and nutrient supply is obviously more favorable for blood parasites than for those of the gut. However, it may indeed be the conditions within the shad gut that favor maturation in *T. longirostris*. As mentioned earlier, alternating planktivory and herbivory in shad may ultimately increase the chance of successful maturation. The intestinal environment of the shad may provide a more suitable array of nutrients and spectrum of enzymatic activity than is found in obligate carnivores. The latter usually exhibit sporadic (opportunistic) feeding, that is periods when the gut is packed with animal material, alternating with periods of depleted gut contents. For example, I have found the digestive tracts of spotfin shiners (*Notropis spilopterus*), white crappie, and bluegill sunfish filled with planktonic crustaceans at certain times and totally empty at others. Likewise, on occasion, the same species contained 40 or 50 immature stages of *T. longirostris*. None of the worms were ever found to be approaching sexual maturity. Whereas small white crappies often contain large numbers of young worms, I have not found worms of any stage in crappies larger than 10 cm TL. This is consistent with the data of O'Brien and Wright (1985), who proposed that white crappies at about 10 cm TL change from feeding on zooplankton to fish and benthic invertebrates. Jilek (1978) reported the presence of *T. longirostris* (all worms were dead) in white crappies, but did not comment on the size of the hosts.

SUMMARY

Van Cleave (1931) commented on apparent host specificity of *T. longirostris* for shad of the genus *Dorosoma*. Data from numerous studies conducted since then support that observation. Although no single one of the five factors proposed by Shulman (1954) can account for the relationship, neither can any of these be ruled out. The inability to satisfy these factors at this time is related to the lack of enough specific information from which to draw conclusions. However, because strong host-specificity is apparent, I suggest that the relationship between *T. longirostris* and its shad hosts is a young and developing one. As such, opportunity for successful adaptation to other possible hosts has been limited in both time and space.

The notion of host specificity for *T. longirostris* in the calanoid copepod *Diaptomus pallidus*, is supported by field data. In this study, of the 15 species of planktonic crustaceans that occurred in the Caesar Creek Lake community, *D. pallidus* alone contained the cystacanths of *T. longirostris*.

The evidence for specificity in shad is equally strong. Live or sexually mature specimens of *T. longirostris* are usually found only in shad. Minor exceptions in the record are rare and unusual. Whenever the immature worm has been found in any other fish species, infected shad have always been members of the same community. Finally, the distribution record of *T. longirostris* does not exceed the known ranges of both shad and the copepod host.

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LITERATURE CITED

Amin, O. M. 1985 Classification. *In*: D. W. T. Crompton and B. B. Nickol (eds.) Biology of the Acanthocephala. Cambridge,. p. 67.

Arnold, J. G., Jr., H. E. Schafer, and R. L. Vulliet 1968 The parasites of the fresh water fishes of Louisiana. II. Check List of Parasites. Proc. (21) Ann. Conf. Southeast Assn. Game and Fish Comm. pp. 531-543.

Bangham, R. V. 1972 A resurvey of the fish parasites of Western Lake Erie. Bull. Ohio Biol. Surv. Vol. 4, No. 2 (New Series), 23 pp.

——— and C. E. Venard 1942 Studies on parasites of Reelfoot Lake fish. IV. Distribution studies and checklist of parasites. Jour. Tenn. Acad. Sci. 17: 22-38.

Bodola, A. 1966 Life history of the gizzard shad, *Dorosoma cepedianum* (Lesueur), in Western Lake Erie. Bull. U.S. Fish and Wildlife Serv. 65: 391-425.

Brooks, J. L. and S. I. Dodson 1965 Predation, body size, and composition of plankton. Science 150: 28-35.

Chandler, A. C. 1935 Parasites of fishes in Galveston Bay. Proc. U.S. Nat. Mus. 83(2977): 123-157.

Cramer, J. D. and G. R. Marzolf 1970 Selective predation on zooplankton by gizzard shad. Trans. Amer. Fish Soc. 99: 320-332.

Dechtiar, A. O. 1972 New parasite records for Lake Erie fish. Great Lakes Fish. Comm. 20 p.

Drenner, R. W., F. deNoyelles, Jr., and D. Kettle 1982 Selective impact of filter-feeding gizzard shad on zooplankton community structure. Limnol. Oceanogr. 27: 965-968.

Gunter, G. 1945 Studies on Marine Fishes of Texas. Inst. Marine Sci. Univ. Texas, Austin 1(1): 1-190.

Hairston, N. G., Jr., K. T. Li, and S. S. Easter, Jr. 1982 Fish vision and the detection of planktonic prey. Science 218: 1240-1242.

Heinrichs, S. M. 1982 Ontogenetic changes in the digestive tract of the larval gizzard shad, *Dorosoma cepedianum*. Trans. Amer. Micro. Soc. 101: 262-275.

Hopkins, S. H. 1966 A comparison of the parasites of two freshwater shads, *Dorosoma (Dorosoma) cepedianum* and *Dorosoma (Signalosa) petenense*, in Lake Texoma. J. Parasit. 52: 843.

Houde, E. D. 1967 Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York. Trans. Amer. Fish. Soc. 96: 17-24.

Hubschman, J. H. 1983 *Diaptomus pallidus* Herrick 1879 (Crustacea: Copepoda) as an intermediate host for *Tanaorhamphus longirostris* (Van Cleave, 1913) (Acanthocephala: Neoechinorhynchidae). J. Parasit. 69: 930-932.

——— 1985 *Tanaorhamphus longirostris* (Acanthocephala) in gizzard shad from Caesar Creek Lake, Ohio. Ohio J. Sci. 85: 7-11.

Jester, D. B. and B. L. Jensen 1972 Life history and ecology of the gizzard shad *Dorosoma cepedianum* (Lesueur), with reference to Elephant Butte Lake. Agr. Exp. Sta. Res. Rep. #218. New Mexico State Univ., Las Cruces, New Mexico pp. 42-44.

Jilek, R. 1978 Seasonal occurrence and host specificity of *Gracilisentis gracilisentis* and *Tanaorhamphus longirostris* (Acanthocephala: Neoechinorhynchidae) in Crab Orchard Lake, Illinois. J. Parasit. 64: 951-952.

King, P. A., T. E. Wissing, E. J. DeVillez, M. J. Chimney, and W. B. Randall, Jr. 1977 Nutritional implications of surface feeding by gizzard shad (*Dorosoma cepedianum*) on insect remains in an Ohio reservoir. J. Fish. Res. Bd. Can. 34: 269-273.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980 Atlas of North American Freshwater Fishes. Pub. #1980-12, N. Carolina Biol. Surv. p. 69.

Muzzall, P. M. and F. C. Rabalais 1975 Studies on *Acanthocephalus jacksoni* Bullock, 1962 (Acanthocephala: Echinorhynchidae). III. The altered behavior of *Lirceus lineatus* (Say) infected with cystacanths of *Acanthocephalus jacksoni*. Proc. Helm. Soc. Wash. 42: 116-118.

O'Brien, W. J. and D. I. Wright 1985 Potential limits on the daytime planktivorous feeding depth of white crappie. Verh. Internat. Verein. Limnol. 22: 2527-2533.

Pierce, R. J. and T. E. Wissing 1981 Aspects of the feeding ecology of gizzard shad in Acton Lake, Ohio. Trans. Amer. Fish. Soc. 110: 391-395.

Price, R. L. and R. Jilek 1980 Parasites of the gizzard shad, *Dorosoma cepedianum* Lesueur, from two southern Illinois lakes. Trans. Ill. State Acad. Sci. 72: 51-52.

Read, C. P. 1972 Animal Parasitism. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 182 pp.

Robertson, A. and J. E. Gannon 1981 Annotated checklist of the free-living copepods of the Great Lakes. J. Great Lakes Res. 7: 382-393.

Samuel, N., B. B. Nickol, and M. A. Mayes 1976 Acanthocephala of Nebraska fishes. Amer. Mid. Nat. 96: 391-406.

Schmitz, E. H. and C. D. Baker 1969 Digestive anatomy of the gizzard shad, *Dorosoma cepedianum* and the threadfin shad, *D. petenense*. Trans. Amer. Micro. Soc. 88: 525-546.

Scott, W. B. and E. J. Crossman 1973 Freshwater Fishes of Canada. Bull. 184, Fish. Res. Bd. Can. Ottawa. p. 605.

Seidenberg, A. J. 1973 Ecology of the acanthocephalan, *Acanthocephalus dirus* (Van Cleave, 1931), in its intermediate host, *Asellus intermedius* Forbes (Crustacea: Isopoda). J. Parasit. 59: 957-962.

Shulman, S. S. 1954 Concerning the specificity of fish parasites. Zoologicheskii Zhurnal 33: 14-25. W. E. Ricker, Fish. Res. Bd. of Can. Translation Series, No. 177, 1958.

Smith, K. and C. H. Fernando 1978 A Guide to the Freshwater Calanoid and Cyclopoid Copepod Crustacea of Ontario. Univ. Waterloo Biol. Series, No. 18, 76 pp.

Van Cleave, H. J. 1913 The genus *Neorhynchus* in North America. Zoologischer Anzeiger 43: 177-190.

——— 1916 Seasonal distribution of some Acanthocephala from fresh-water hosts. J. Parasit. 2: 106-110.

——— 1931 New Acanthocephala from fishes of Mississippi and a taxonomic reconsideration of forms with unusual numbers of cement glands. Trans. Amer. Micro. Soc. 50: 348-363.

Watson, N. H. F. 1976 Seasonal distribution and abundance of crustacean zooplankton in Lake Erie, 1970. J. Fish. Res. Bd. Can. 33: 612-621.

Wilson, B. A. and J. H. Hubschman 1985 Host-parasite relationships of *Tanaorhamphus longirostris* (Acanthocephala: Neoechinorhynchidae) in the intermediate host, *Diaptomus pallidus* (Crustacea: Copepoda). Proc. Helm. Soc. Wash. 52: 71-75.